Journal of Archaeological Science 30 (2003) 1665–1671

Journal of Archaeological SCIENCE

http://www.elsevier.com/locate/jas

Fragmentation and preservation of bird bones in uneaten food remains of the Gyrfalcon *Falco rusticolus*

Zbigniew M. Bochenski [a]*, Risto Tornberg [b]

[a] *Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Slawkowska 17, 31-016 Kraków, Poland*
[b] *Zoological Museum, University of Oulu, POB 333, 90571 Oulu, Finland*

Received 17 December 2002; received in revised form 1 May 2003; accepted 1 May 2003

Abstract

This paper presents fragmentation patterns of bird bones in uneaten food remains of the gyrfalcon *Falco rusticolus*. The victims' bones show a relatively low degree of fragmentation. Elements of the pectoral girdle and wing predominate while head and leg elements are poorly represented.

Keywords: Taphonomy; Bird bones; Food remains; Gyrfalcon; *Falco rusticolus*

1. Introduction

There are several reasons that make the taphonomic analysis of gyrfalcons' food remains of special interest. First, gyrfalcons feed mainly on birds, and their favourite prey is the willow grouse, *Lagopus lagopus*, and the rock ptarmigan, *L. mutus* [13,15,17]. Second, remains of the *Lagopus* species are frequently found in Late Pleistocene and Holocene sites of the Palearctic [2,23]. Therefore, the present study may be helpful in determining the factor(s) responsible for the accumulation of fossil and archaeological assemblages. Although gyrfalcons do not nest in caves (from where most fossils come), their food remains may fall into caves and accumulate there [3]. This paper describes the signature left by gyrfalcons on their uneaten bird remains, and refines the classification of predators proposed by Andrews [1].

2. Material and methods

The material was collected from beneath roosts and aeries of gyrfalcons in SE Finnish Forest Lapland during the following five years: 1986 and 1988 through 1991. In this study, only uneaten food remains were examined; pellets have been studied previously [7].

Of the 4093 bones recovered, 2384 (58%) belonged to the two species of the genus *Lagopus* (willow grouse and/or rock ptarmigan). The remaining bones represent a variety of taxa and are treated jointly as "other prey". Eighty percent of this grouping is made up of charadrids (*Numenius*, *Pluvialis*, *Larus*), while the remaining taxa include black grouse, capercaillie, crow and owls. Many wing and leg elements were found still in articulation, often covered with skin, feathers and horny coverings, so that only parts of the bones were visible.

Bones were categorized into classes of fragmentation, as proposed by Bochenski et al. [6: figures 1–5]. Bones from the left and right side of the body were pooled within each category.

The proportion of proximal and distal parts of bones was calculated from the total number of proximal and distal fragments (i.e., whole bones plus proximal parts and whole bones plus distal parts).

Bone ratio of the wing to leg elements was calculated as the number of wing fragments (humerus, ulna, carpometacarpus) divided by the sum of wing and leg fragments (femur, tibiotarsus, tarsometatarsus), expressed as percentage [14,20].

* Corresponding author
E-mail address: bochenski@isez.pan.krakow.pl
(Z.M. Bochenski).

0305-4403/03/$ - see front matter
doi:10.1016/S0305-4403(03)00069-4

Table 1
Fragmentation of the skull, mandible, sternum and pelvis in food remains of the gyrfalcon (for categories of fragmentation see [6: figs 1–4])

Skull

Number of fragments	Whole skull %	Skull with beak and brain case without back part %	Brain case without back part %	Brain case %	Whole beak %	End of beak %	Other fragments %	MNE %	Element MNI N	Total MNI (%)
Lagopus, *N*=0	0	0	0	0	0	0	0	0	0	0
Other, *N*=12	33	0	0	25	25	0	17	0.4	7	7
Total, *N*=12	33	0	0	25	25	0	17	0.2	7	2

Mandible

Number of fragments	Whole %	One branch %	Articular part %	Tip of mandibula %	Middle part of branch %	MNE %	Element MNI N	Total MNI%
Lagopus, *N*=0	0	0	0	0	0	0	0	0
Other, *N*=7	57	14	0	29	0	0.4	6	6
Total, *N*=7	57	14	0	29	0	0.2	6	2

Sternum

Number of fragments	More than half with rostrum %	Less than half with rostrum %	Fragments without rostrum %	MNE %	Element MNI N	Total MNI %
Lagopus, *N*=235	31	57	11	10	208	100
Other, *N*=91	30	58	12	5	80	78
Total, *N*=326	31	58	12	8	288	100

Pelvis

Number of fragments	Synsacrum with 1 or 2 ilium–ischii–pubis bones %	Ilium–ischii–pubis bone %	Synsacrum whole or partial %	Acetabulum region %	MNE %	Element MNI N	Total MNI %
Lagopus, *N*=132	23	5	45	26	4	91	44
Other, *N*=56	48	4	20	29	2	38	37
Total, *N*=188	31	5	38	27	3	129	45

MNE is the minimum number of elements. Total MNI% is the percentage that the Element MNI represents of the Total MNI for the fauna (in "*Lagopus*" and "Total"—obtained from the sternum, in "Other"—obtained from the humerus).

Bone ratio of the proximal to distal elements was calculated as the number of proximal fragments (scapula, coracoideum, humerus, femur, tibiotarsus) divided by the sum of proximal and distal fragments (ulna, radius, carpometacarpus, tarsometatarsus), expressed as percentage [10].

Bone ratio of the "core" to "limb" elements was calculated as the number of the "core" fragments (sternum, pelvis, scapula, coracoideum) divided by the sum of core and "limb" fragments (humerus, ulna, radius, carpometacarpus, femur, tibiotarsus, tarsometatarsus), expressed as percentage [12].

A chi-square test was used to evaluate the significance of differences in survivorship of particular skeletal elements or their fragments.

The minimum number of individuals (MNI) was calculated for each element separately. The results are presented as absolute numbers (i.e., Element MNI) and as percentages of the number of fragments of the element which provided the highest value of the MNI (i.e., Total MNI%). The MNI values are certainly underestimated because they were calculated from all pooled material (i.e., not from each year separately), bones were not determined to species (they were only divided into *Lagopus* and "other prey"), and proximal and distal parts were not fitted together. The same procedure was used in previous studies [4–11]. This procedure saves much time and the error is believed to be similar for each type of element.

The minimum number of elements (MNE) was calculated in a similar way to the MNI: the number of complete bones and that of proximal or distal parts of the left or right side—whichever was more numerous—were used in this calculation [21].

3. Results

3.1. Fragmentation patterns

3.1.1. Axial skeleton

Fragments of skulls and mandibles are very scarce in the material, and the few remains recovered belong in the category "other prey" (Table 1). On the contrary, remains of the sternum are very numerous in both groups of prey.

In comparison to long bones, elements of the axial skeleton (if they are present at all) show a relatively high degree of fragmentation (Fig. 1).

3.1.2. Long bones

The most numerous fragments of long bones are those of the pectoral girdle and wings, whereas legs are poorly represented (Table 2).

Food remains of gyrfalcons show relatively low degree of fragmentation, as the proportion of whole elements often exceeds 60% (Fig. 1). However, particular skeletal elements differ very much in the degree of fragmentation. The most affected bones are scapulae (the share of whole bones is less than 10%) followed by tibiotarsi, femora and radii, whereas the least fragmented bones are carpometacarpi and tarsometatarsi (where the amount of whole bones is more than 90% each).

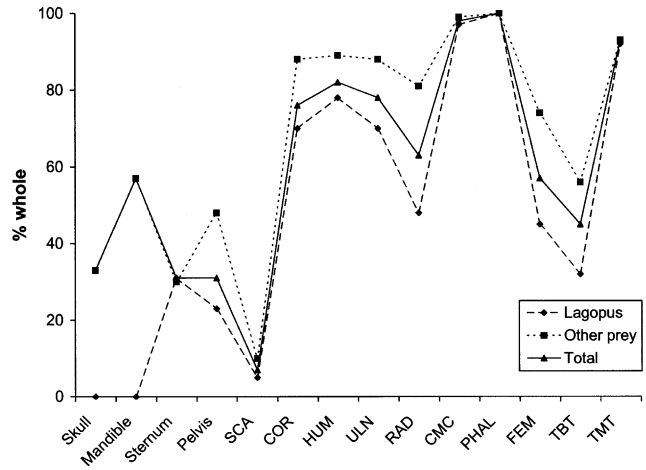

Fig. 1. Percentage of complete (i.e. not broken) long bones in uneaten food remains of gyrfalcons. SCA—scapula, COR—coracoideum, HUM—humerus, ULN—ulna, RAD—radius, CMC—carpometacarpus, FEM—femur, TBT—tibiotarsus, TMT—tarsometatarsus.

The two groups of prey ("*Lagopus*" and "other prey") generally exhibit a similar degree of fragmentation in particular elements, the largest differences being in radii, femora and tibiotarsi while the smallest differences are observed in the most heavily fragmented scapula and the least fragmented carpometacarpi and tarsometatarsi. In all cases *Lagopus* is more affected than "other prey".

Statistically significant differences in the preservation of proximal and distal ends are found in three elements only: *Lagopus*—in ulnae and radii (proximal ends more numerous), and "other prey"—in tibiotarsi (distal ends more numerous) (Table 2: columns 2+3 versus 2+4).

Shafts of long bones separated from articular ends (Table 2: column 5) were practically non-existent in the material.

3.1.3. Wing/leg ratio

Wing bones represented 70% of the sum of wing and leg bones in "other prey", 76% in *Lagopus*, and 74% in the entire sample. In all cases, the deviation from the expected 50% (1:1 proportion) was found to be statistically highly significant (P<0.01, df=1).

3.1.4. Proximal elements/distal elements ratio

Proximal elements of the skeleton represented 53% of the sum of proximal and distal elements in "other prey", 64% in *Lagopus*, and 59% in the entire sample. In all cases, the predominance of proximal elements was found to be statistically significant (P<0.01, df=1).

Table 2
Fragmentation of long bones in food remains of the gyrfalcon expressed as percentages of the total number of fragments for the element found (for categories of fragmentation see [6: fig. 5])

Bones (total number of fragments)		Whole bone %	Proximal part %	Distal part %	Shaft %	MNE %	Element MNI N	Total MNI %
1		2	3	4	5	6	7	8
Scapula	*Lagopus*, *N*=313	5	95	0	0.3	14	160	77
	Other, *N*=180	10	90	0	0	11	91	89
	Total, *N*=493	7	93	0	0.2	13	251	87
Coracoideum	*Lagopus*, *N*=359	70	11	19	0	15	166	80
	Other, *N*=187	88	2	10	0	11	92	90
	Total, *N*=546	76	8	16	0	13	258	90
Humerus	*Lagopus*, *N*=356	78	15	6	1	15	170	82
	Other, *N*=210	89	8	3	0.5	12	102	100
	Total, *N*=566	82	12	5	1	14	272	94
Ulna	*Lagopus*, *N*=238	70	26*	4	0	10	125	60
	Other, *N*=193	88	9	3	0	11	95	93
	Total, *N*=431	78	18*	4	0	11	217	75
Radius	*Lagopus*, *N*=233	48	43*	9	0	10	114	55
	Other, *N*=191	81	10	9	0	11	89	87
	Total, *N*=424	63	28*	9	0	10	203	70
Carpometacarpus	*Lagopus*, *N*=150	97	2	1	0	7	77	37
	Other, *N*=177	99	1	0	0	11	91	89
	Total, *N*=327	98	2	0.3	0	8	168	58
Phalanx I dig maj. alae	*Lagopus*, *N*=138	100	0	0	0	6	71	34
	Other, *N*=160	100	0	0	0	10	82	80
	Total, *N*=298	100	0	0	0	8	153	53
Femur	*Lagopus*, *N*=92	45	39	16	0	4	41	20
	Other, *N*=63	74	19	6	0	4	31	30
	Total, *N*=155	57	31	12	0	4	69	24
Tibiotarsus	*Lagopus*, *N*=77	32	31	36	0	2	32	15
	Other, *N*=91	56	4	40*	0	5	49	48
	Total, *N*=168	45	17	38*	0	4	70	24
Tarsometatarsus	*Lagopus*, *N*=61	92	0	8	0	3	38	18
	Other, *N*=91	93	3	3	0	5	48	47
	Total, *N*=152	93	2	5	0	4	79	27

In scapula: distal part and shaft are shown jointly in the category "shaft". In coracoideum: proximal=sternal, distal=scapular. For MNE, Element MNI and Total MNI%, see Table 1.

*indicates statistically significant predominance of proximal ends (whole bones+proximal parts) or distal ends (whole bones+distal parts).

3.1.5. Core elements/limb elements ratio

Core elements of the skeleton represented 34% of the sum of core and limb elements in "other prey", 46% in *Lagopus*, and 41% in the entire sample. The under-representation of core elements was found to be statistically significant ($P<0.01$, df=1).

3.1.6. Minimum number of individuals

The element MNI, and the percentage it represents of Total MNI for the fauna are listed for each element separately (Tables 1 and 2: two last columns; Fig. 2). In *Lagopus*, the highest value for the MNI was obtained for the sternum (Element MNI=208, Total MNI=100%) whereas in "other prey" it was for the humerus (Element MNI=102, Total MNI=100%). Generally, the two groups of prey provided similar data. Values of Total MNI were low for the skull, mandible and leg elements, whereas those for the sternum, pectoral girdle and wing bones were much higher. With one exception (sternum) "other prey" provided higher values of the Total MNI than *Lagopus*; the largest differences (of about 30 or more percent) between the two groups of prey were observed in the distal elements of the wing (ulna, radius, carpometacarpus, phalanx I) and in the distal elements of the leg (tibiotarsus, tarsometatarsus).

3.1.7. Minimum number of elements

The proportion of particular elements in both groups of prey (*Lagopus* and "other prey") is very similar (Tables 1 and 2; Fig. 3). The highest values were obtained with the scapula, coracoid and wing elements, and the lowest with the skull, mandible, pelvis and leg elements. A noteworthy difference between *Lagopus* and "other prey" was observed only for the sternum (in

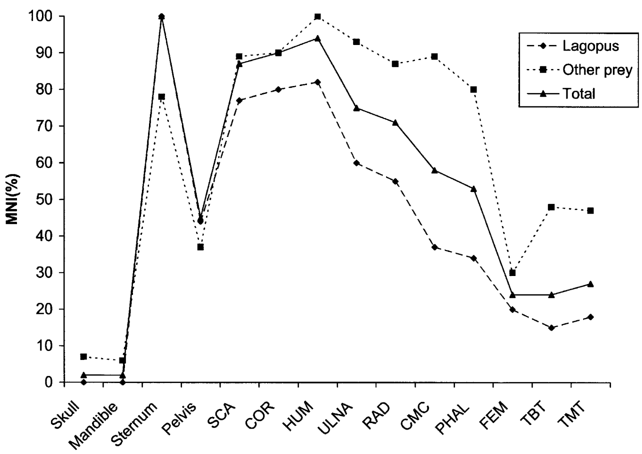

Fig. 2. Total MNI% for skeletal elements in uneaten food remains of gyrfalcons. Abbreviations as in Fig. 1.

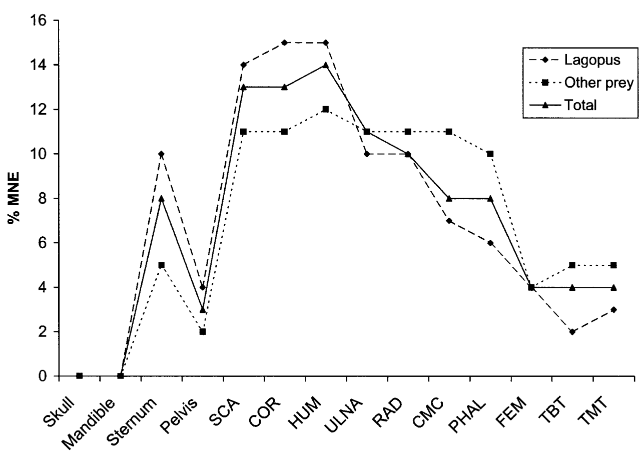

Fig. 3. Share of particular elements (%MNE) in uneaten food remains of gyrfalcons. Abbreviations as in Fig. 1.

Lagopus it was well represented whereas in "other prey" it scored poorly).

3.1.8. Perforation of bones

Small punctures (one or more on the same element) were observed on 3% of coracoids and 15% of humeri (Table 3, Fig. 4). Most of the punctures vary in size and were near articular ends of the bones. A great majority of bones damaged in this way belonged to *Lagopus*.

4. Discussion and comments

The present material has been included in a detailed study comparing "signatures" of all avian predators studied so far [5]. Therefore, such a comparison will not be repeated here. It is sufficient to say that particular analyses (including degree of fragmentation, wing/leg ratio, proximal elements/distal elements ratio, core elements/limb elements ratio, MNI, MNE) have shown that the material analysed here is most similar to uneaten food remains of other diurnal birds of prey and it clearly differs from pellet samples of owls and raptors.

The results from this study indicate that the classification of predators based on the degree of damage imposed on the bones of their prey [1], should be refined. Andrews [1], analysing pellets, placed diurnal birds of prey in a separate category from owls based upon the notion that diurnal birds of prey produce more post-cranial fragmentation. However, bones of prey recovered from uneaten food remains of imperial eagles [9], golden eagles [8] and gyrfalcons (this study) are less damaged and fragmented than those from pellets of owls and other raptors.

The differences between particular skeletal elements in the degree of fragmentation are probably related to their physical properties. Scapulae and tibiotarsi (heavily damaged) are very fragile while carpometacarpi and tarsometatarsi (little damaged) are stout and therefore less prone to fragmentation. Although the long, thin shafts of radii are also very fragile, they suffer relatively little damage, most probably because they are protected by robust ulnae. The little fragmentation of coracoids and wing elements may be explained by the fact that diurnal raptors strip meat off from their prey, often leaving the pectoral girdle in articulation (sternum–coracoid–humerus).

It is also tempting to explain the differences between *Lagopus* and "other prey" in preservation and fragmentation of particular elements with physical properties of the victims' bones. However, the problem is more complicated. Charadrids, which constituted a large part of "other prey", have generally thinner and more elongated (i.e., more fragile) limb bones than *Lagopus*, yet they suffer less fragmentation. It is likely that this may be due to "biological factors". Charadrids and other smaller prey were foraged mainly by chicks and fledglings gyrfalcons, while *Lagopus* were mostly preyed upon by adult birds. Thus, the differences may be due to foraging behaviour by the two age classes of the same predator.

Table 3
Number of bones with holes near articular ends (see also Fig. 4)

Taxa	Coracoid		Humerus	
	N	% bones with holes	*N*	% bones with holes
Lagopus	16	3	69	12.2
Lyrurus tetrix	–	–	3	0.5
Charadriiformes	–	–	11	2
Owl	–	–	1	0.2
Total	16	3	84	15

Fig. 4. Damage to bones done by gyrfalcons. A—general view; punctures are usually near articular ends; B–C—details of the 1st and 4th bones from left.

Remains of crania (skulls and mandibles) are extremely rare in pellets [7] and uneaten food remains of gyrfalcons (present study). This is because the raptors decapitate their prey where it is killed [3,16,22,24]. Similar scarcity of cranial remains was observed also in pellets of eagle owls [6] and uneaten food remains of golden eagles [8]. It is noteworthy that in the gyrfalcon sample (this study), remains of skulls and mandibles are

found exclusively in the "other prey" category. Even so, cranial remains are too scarce to reach a meaningful conclusion.

Perforation of bones observed in this study is consistent with that described by Laroulandie [18,19] for pellets of eagle owls and food remains of peregrine falcons. In all cases, punctures are located near the articular ends, and the humerus is the most frequently affected element. Although the share of bones damaged in this way is different in each of the three species (eagle owls, peregrine falcons and gyrfalcons), the samples are too small to generalize about them at this stage. Perforation of bones seems to take place when the prey is too large to be swallowed whole and the raptor has to tear it apart. Further studies are needed to explain how the punctures are made (e.g., with beak or claw), which raptors do (and which do not) leave such traces, and whether the differences between species are distinctive enough to tell them apart. In any case, it seems that perforation of bones (visible especially often on the humerus) should be included in taphonomic studies of archaeological and fossil assemblages.

Acknowledgement

We are thankful to Mr Christopher A. Shaw (George C. Page Museum) for correcting the language of this paper.

References

[1] P. Andrews, Owls, caves and fossils. Predation, preservation and accumulation of small mammal bones in caves, with an analysis of the Pleistocene cave faunas from Westbury-sub-Mendib, Somerset, UK, Natural History Museum Publications, London, 1990, pp. 231.

[2] M. Baales, Accumulation of bones of Lagopus in Late Pleistocene sediments. Are they caused by man or animals?, Cranium 9 (1) (1992) 17–22.

[3] S.A. Bengston, Hunting methods and choice of prey of gyrfalcons *Falco rusticolus* at Myvatn in Northeast Iceland, Ibis 113 (1971) 468–476.

[4] Z.M. Bochenski, Preliminary taphonomic studies on damage to bird bones by Snowy Owls *Nyctea scandiaca*, with comments on the survival of bones in palaeontological sites, Acta zoologica cracoviensia 40 (2) (1997) 279–292.

[5] Z.M. Bochenski, Owls, diurnal raptors and humans: signatures on avian bones, in: T. O'Connor (Ed.), Biosphere to Lithosphere: New Studies in Vertebrate Taphonomy, Oxbow, in press.

[6] Z.M. Bochenski, Z. Boev, I. Mitev, T. Tomek, Patterns of bird bone fragmentation in pellets of the Tawny Owl (*Strix aluco*) and the Eagle Owl (*Bubo bubo*) and their taphonomic implications, Acta zoologica cracoviensia 36 (2) (1993) 313–328.

[7] Z.M. Bochenski, K. Huhtala, P. Jussila, E. Pulliainen, R. Tornberg, P.S. Tunkkari, Damage to bird bones in pellets of Gyrfalcon *Falco rusticolus*, Journal of Archaeological Science 25 (1998) 425–433.

[8] Z.M. Bochenski, K. Huhtala, S. Sulkava, R. Tornberg, Fragmentation and preservation of bird bones in food remains of the Golden Eagle *Aquila chrysaetos*, Archaeofauna 8 (1999) 31–39.

[9] Z.M. Bochenski, V.A. Korovin, A.E. Nekrasov, T. Tomek, Fragmentation of bird bones in food remains of Imperial Eagles *Aquila heliaca*, International Journal of Osteoarchaeology 7 (2) (1997) 165–171.

[10] Z.M. Bochenski, A.E. Nekrasov, The taphonomy of Sub-Atlantic bird remains from Bazhukovo III, Ural Mountains, Russia, Acta zoologica cracoviensia 44 (2) (2001) 93–106.

[11] Z.M. Bochenski, T. Tomek, Pattern of bird bone fragmentation in pellets of the Long-eared Owl *Asio otus* and its taphonomic implications, Acta zoologica cracoviensia 37 (1) (1994) 177–190.

[12] D. Bramwell, W. Yalden, P.E. Yalden, Black grouse as the prey of the golden eagle at an archaeological site, Journal of Archaeological Science 14 (1987) 195–200.

[13] S. Cramp, K.E.L. Simmons, The Birds of the Western Palearctic II, Oxford University Press, Oxford, London, New York, 1980, pp. 695.

[14] P.G.P. Ericson, Interpretations of archaeological bird remains: A taphonomic approach, Journal of Archaeological Science 14 (1987) 65–75.

[15] U.N. Glutz von Blotzheim, K.M. Bauer, E. Bezzel (Eds.), Handbuch der Vögel Mitteleuropas IV, Akademische Verlagsgesellschaft, Frankfurt/M, 1971, pp. 943.

[16] Y. Hagen, The gyrfalcon (*Falco r. rusticolus* L.) in Dovre, Norway. Some breeding records and food studies, Skrifter utgitt av Det Norske Videnskaps—Akademi i Oslo Matematisk—Naturvidenskapelig Klasse 4 (1952) 1–37.

[17] K. Huhtala, E. Pulliainen, P. Jussila, P.S. Tunkkari, Food niche of the gyrfalcon *Falco rusticolus* nesting in the far north of Finland as compared with other choices of the species, Ornis Fennica 73 (1996) 78–87.

[18] V. Laroulandie, Taphonomie et archéozoologie des oiseaux en grotte: applications aux sites Paléolithiques du Bois-Ragot (Vienne), de Combe Saunière (Dordogne) et de la Vache (Ariège). Thèse d'Université, Université de Bordeaux I. Pdf document is available (ask by mail), 2000.

[19] V. Laroulandie, Damage to pigeon long bones in pellets of the eagle owl *Bubo bubo* and food remains of peregrine falcon *Falco peregrinus*: zooarchaeological implications, in: Z.M. Bochenski, Z. Bochenski, J.R. Stewart (Eds) Proceedings of the 4th Meeting of the ICAZ Bird Working Group, Kraków, Poland, 11–15 September, 2001. Acta zoologica cracoviensia 45(special issue) (2002) 331–339.

[20] S.D. Livingston, The taphonomic interpretation of avian skeletal part frequencies, Journal of Archaeological Science 16 (1989) 537–547.

[21] R.L. Lyman, Vertebrate Taphonomy. Cambridge Manuals in Archaeology, Cambridge University Press, Cambridge, 1994, pp. 524.

[22] G.H. Scherlock, Beobachtungen am Horst des Isländischen Jagdfalken, Journal für Ornithologie 88 (1940) 136–138.

[23] T. Tyrberg, Palaeobiogeography of the genus *Lagopus* in the West Palaearctic, Courier Forschungsinstitut Senckenberg 181 (1995) 275–291.

[24] P. Wayre, G.F. Jolly, Notes on the breeding of the Iceland gyrfalcon, British Birds 51 (1958) 285–290.